THE EARLIEST KNOWN FENESTRATE BRYOZOAN, WITH A SHORT REVIEW OF LOWER ORDOVICIAN BRYOZOA

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ABSTRACT. Silicified residues from the late Arenig Tourmakeady Limestone of County Mayo, Ireland, contain a new bryozoan, *Alwynopora orodamnus* gen. et sp. nov. Colonies have erect branches bearing two rows of alternating zooecial apertures on their frontal surface and barren of apertures on their reverse surface. Branches bifurcate irregularly, successive bifurcations tending to be approximately in the same plane. There is a strong gradient of branch thickening towards the colony base. *Alwynopora* is the earliest known bryozoan of the Order Fenestrata. The occurrence of bryozoans in the lower Ordovician is briefly reviewed; the thirty-eight taxa described have an extensive taxonomic distribution, are morphologically diverse, and geographically widespread.

THE Fenestrata are regarded as a distinct order of stenolaemate bryozoans in the revised *Treatise on invertebrate paleontology* (Boardman *et al.* 1983), although some bryozoologists argue for their retention as a suborder of the Cryptostomata (Blake *in* Boardman *et al.* 1983). Most fenestrates are readily recognizable by their reticulate or pinnate colonies with zooecial apertures opening on one side of the branches only. Fenestrate bryozoans peaked in diversity during the late Palaeozoic when members of the families Fenestellidae and Acanthocladiidae dominated the majority of bryozoan faunas. However, the origins of the order may be traced back to the Ordovician. Hitherto the earliest described fenestrate bryozoan dates from the middle Ordovician. The purpose of this paper is to describe the first lower Ordovician fenestrate bryozoan, *A. orodamnus* gen. et sp. nov., from the Tourmakeady Limestone of western Ireland. In the absence of unequivocal Cambrian bryozoans, the earliest bryozoans are a modest number of taxa described from the lower Ordovician. The discovery of this new fenestrate bryozoan adds to the taxonomic distribution, morphological diversity, and geographical range of lower Ordovician bryozoans which are briefly reviewed.

All described material bears British Museum (Natural History) (abbreviated BM (NH)) registration numbers.

GEOLOGICAL SETTING

The lower Ordovician Tourmakeady Limestone (Glensaul Group) of Co. Mayo, Ireland, is of considerable interest not only because of the abundance and diversity of the fossils it contains, but also because this fauna provides a link between contemporaneous American province faunas in Scotland, North America, and Spitsbergen. The stratigraphic setting of the Tourmakeady Limestone within the lower Ordovician inliers north of Lough Mask (text-fig. 1) was first described by Gardiner and Reynolds (1910), although at that time the abundance of the indigenous shelly fossils was not appreciated, and the rich assemblages were not subjected to full taxonomic investigation. Gardiner and Reynolds did, however, recognize the stratigraphic importance of the inliers, and their age determinations were based on lists of graptolitic and shelly faunas collected from various exposures within the Tourmakeady and Glensaul successions. The graptolite faunas have been reinvestigated (Dewey *et al.* 1970) following the discovery of some new localities. In addition, the rich brachiopod faunas have now been studied (Williams and Curry 1984), and descriptions of the associated trilobites are in preparation.
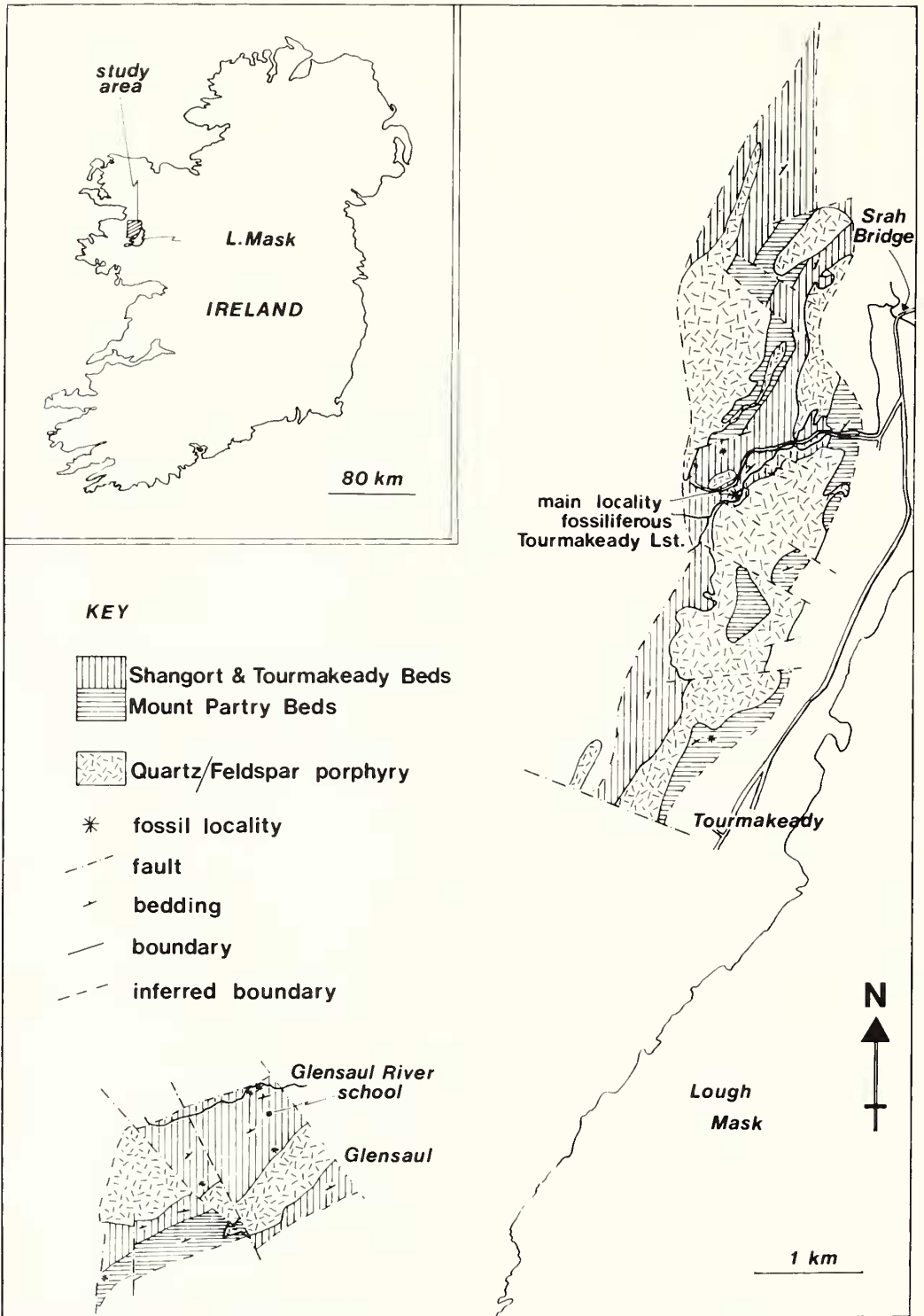
TEXT-FIG. 1. Geological map of the Glensaul Group (Arenig) in Co. Mayo, Eire, showing the Tourmakeady Limestone locality.

The great diversity and abundance of the Tourmakeady Limestone fauna was not fully appreciated until it was discovered that the indigenous fossils have been silicified. As a result, intensive collecting by Sir Alwyn Williams yielded over 2 tons of silicified limestone, which was subsequently etched to give over 10,000 silicified or chitino-phosphatic brachiopods and smaller numbers of silicified trilobites, gastropods, bryozoans, and crinoids. The Tourmakeady Limestone occurs as isolated blocks within well-bedded calcareous tuffs and grits, which together constitute the Shangort and Tourmakeady Beds of Gardiner and Reynolds (see text-fig. 1). Non-silicified fossils, in particular brachiopods and trilobites, are also found at several localities within the tuff and grit succession, and are conspecific and almost certainly contemporaneous with the silicified fossils in the limestone. However, the non-silicified fossils are generally in a poorer state of preservation, and indeed no well-preserved bryozoans have been recovered from the clastic sediments. The available material, therefore, consists entirely of silicified specimens recovered from etched residues.

Stratigraphically the Tourmakeady Limestone and surrounding sediments occur above an uppermost lower Arenig graptolite assemblage ascribed to the *Isograptus gibberulus* Zone, and are overlain by an upper Arenig assemblage of the *Didymograptus hirundo* Zone (Gardiner and Reynolds 1909, 1910; Dewey *et al.* 1970). This is consistent with age determinations based on the shelly fossils from the Tourmakeady Limestone, which also indicate an upper Arenig age, equivalent to zone K of the North American biostratigraphic succession (see table in Curry *et al.* 1982).

The Tourmakeady Limestone is thought to represent the disrupted remnants of an offshore carbonate buildup, perhaps deposited peripheral to submarine volcanic accumulations (Williams and Curry 1984). The indigenous fauna shows no signs of significant post-mortem transportation, and hence the majority of the benthic animals are assumed to have colonized a fine-grained calcareous mud substrate, subjected to gentle water currents and low to moderate sediment accumulation rates. In keeping with this interpretation, many brachiopods show morphological adaptations for a freelying mode of life (Williams and Curry 1984), while other pedunculate forms can realistically be assumed to have developed modifications of pedicle form to achieve anchorage in fine-grained substrates (as happens in Recent forms, e.g. Curry 1981, 1983).

SYSTEMATIC PALAEONTOLOGY

Indeterminate ?bryozoan

Text-fig. 2A

Material. BM(NH) PD6230.

Description. A poorly preserved fragmentary fossil bearing contiguous, oval-shaped apertures about 0.40×0.25 mm in diameter.

Remarks. This may be a fragment of a bryozoan colony, probably either a cystoporate or a trepostome.

Distribution. Tourmakeady Limestone (upper Arenig), Tourmakeady, Co. Mayo, Eire.

Order FENESTRATA Elias and Condra, 1957
?Family ENALLOPORIDAE Miller, 1889
Genus ALWYNOPORA gen. nov.

Type species. A. *orodamnus* sp. nov.

Derivation of name. After Sir Alwyn Williams who collected the silicified limestone containing this new bryozoan.

Diagnosis. Fenestrata with branches bifurcating irregularly, usually in one plane, anastomosing occasionally, and becoming considerably thickened towards the colony base; two longitudinal rows of alternating zooecial apertures are borne on the frontal surface of each branch.
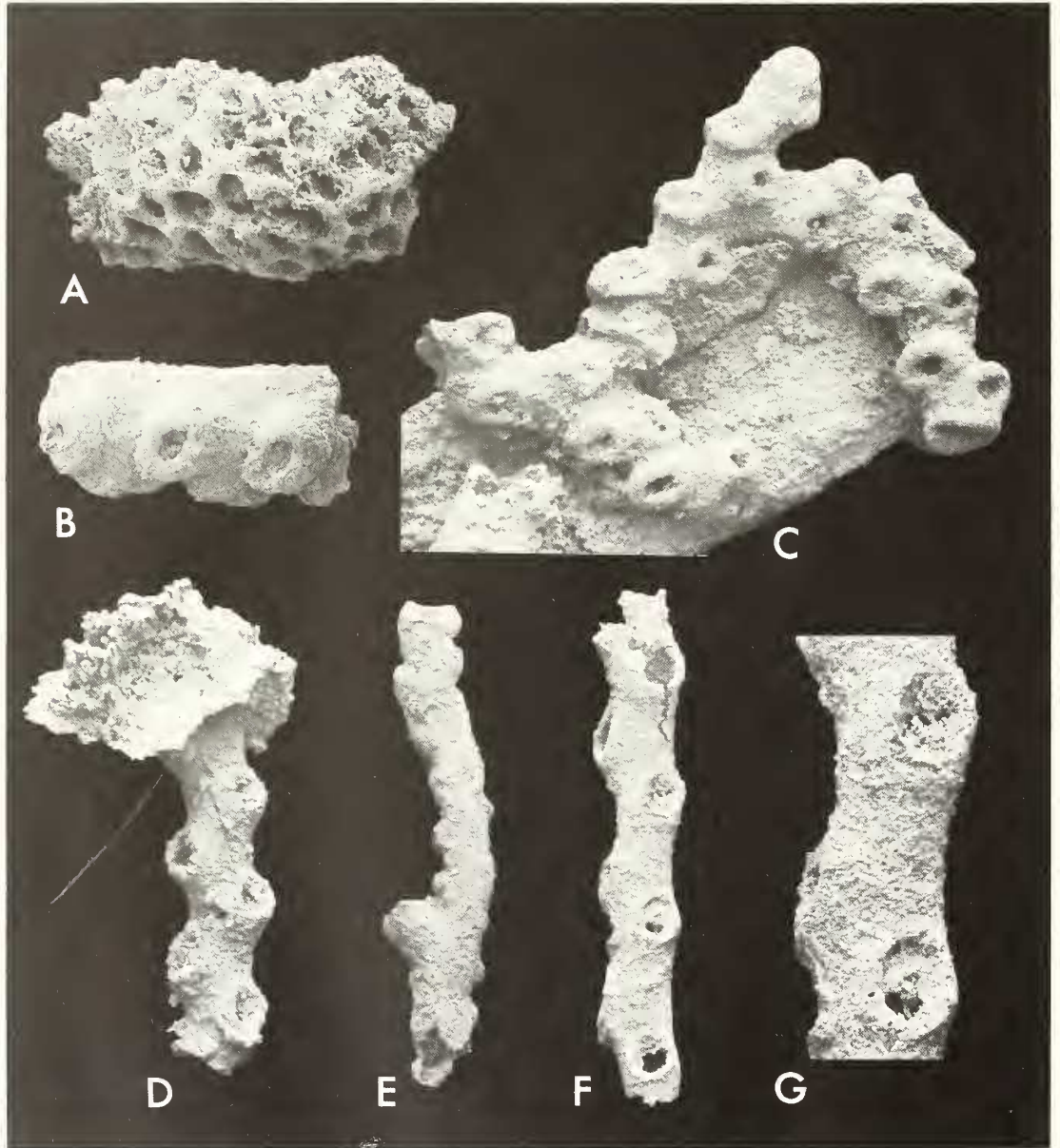
TEXT-FIG. 2. Bryozoans from the Tourmakeady Limestone. A, indeterminate ?bryozoan, BM(NH) PD6230, ×17. B–G, *Alwynopora orodamnus* sp. nov. B, lateral view of compressed branch with frontal surface lowermost, BM(NH) PD6235, ×23; C, bifurcating fragment, BM(NH) PD6241, ×20; D, holotype with encrustation at distal end, BM(NH) PD6231, ×27; E, reverse surface of branch lacking apertures, BM(NH) PD6265, ×10; F, G, frontal surface of narrow, slightly compressed branch, BM(NH) PD6259, F, ×25, G, ×56. (Scanning electron micrographs: A, B, gold-coated specimens using secondary electrons; C–G, uncoated specimens using back-scattered electrons.)

Alwynopora orodamnus sp. nov.

Text-figs. 2B–G, 3, 4

Holotype. BM(NH) PD6231.

Paratypes. BM(NH) PD6232–6272.

Occurrence. Tourmakeady Limestone (upper Arenig), Tourmakeady, Co. Mayo, Eire.

Derivation of name. Orodamnus, Greek meaning bough or branch.

Diagnosis. As for genus.

Description. Colonies have been recovered only as branch fragments which bifurcate unequally or, more rarely, dichotomously. Both bifurcation angle (mean = 50°, range = 30–135° from twenty-one determinations) and interval between bifurcations (mean = 1·73 mm, SD = 0·890 mm, range = 0·40–4·05 mm from nineteen determinations) are very variable. Although anastomoses between branches may be observed, they are neither abundant nor regular. Branches are subcircular to ovoid in transverse section. Two rows of non-contiguous zooecial apertures open on one surface of the branch. Apertures on either side of this frontal surface alternate. Interapertural spacing measured along the branch averages 0·54 mm (SD = 0·088 mm, range = 0·45–0·75 mm from twenty-five colonies). Branch width and depth are highly variable with the thickest branches over three times wider than the thinnest (mean width = 0·62 mm, SD = 0·210 mm, range = 0·32–1·08 mm from twenty-five colonies). Some fragments show a proximal to distal gradient of decreasing branch width. Branch margins are gently sinuous in narrow branches, sinuosities corresponding to the positions of protruberant zooecial apertures, but straight-sided in thick branches. Striae or other branch ornamentation have not been observed. Possible colony bases are slight, flat-bottomed expansions.
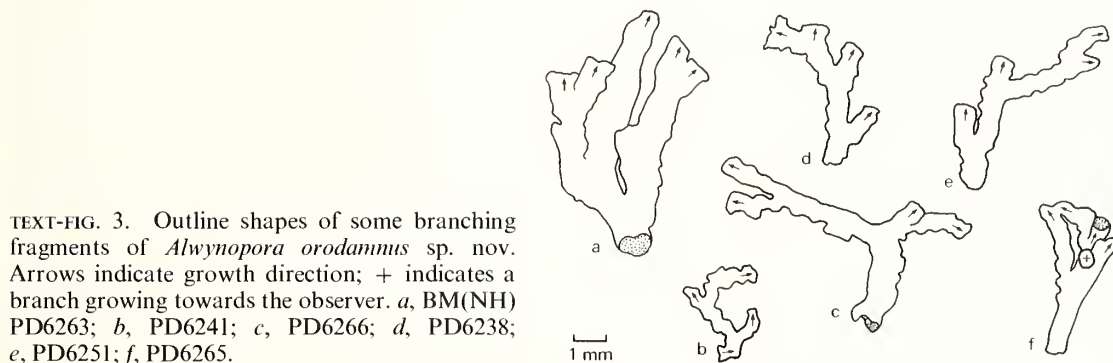

TEXT-FIG. 3. Outline shapes of some branching fragments of *Alwynopora orodamnus* sp. nov. Arrows indicate growth direction; + indicates a branch growing towards the observer. *a*, BM(NH) PD6263; *b*, PD6241; *c*, PD6266; *d*, PD6238; *e*, PD6251; *f*, PD6265.

Zooecial apertures are circular to elliptical in shape and elongated transversely, longitudinally, or obliquely. This apparently depends on preservational factors, several branches showing indications of compression and/or shear. A variably thick rim surrounds each aperture and measurements of apertural width varying between 0·08 and 0·22 mm are similarly dependent on state of preservation. Occlusion of apertures is a characteristic of some branches; this may be due to diaphragm formation or an artefact of silicification. Zooecial chambers are moderately long and have a length that slightly exceeds external interapertural spacing. In shape they are essentially tubular, tapering towards the locus of budding on the midline near the reverse side of the branch. Zooecia were budded alternately left and right of the branch midline, paralleled the branch axis initially, and then turned outwards to meet the colony surface more or less at right angles. Diaphragms and other intrazooecial partitions have not been observed.

Affinities. Delicately branched Ordovician bryozoans exist among three orders, Cyclostomata, Cryptostomata, and Fenestrata. All Ordovician cyclostomes are single-walled stenolaemates *sensu* Borg (1926). These include branching species of *Clonopora* Hall, 1883, *Kukersella* Toots, 1952, *Mitoclema* Ulrich, 1882, *Mitoclemella* Bassler, 1952, and *Wolinella* Dzik, 1981. Here the calcified zooid frontal wall that forms the branch surface is an

exterior wall incapable of adding more calcite to its outer surface. Therefore proximally thickening branches of the kind found in *A. orodamnus* cannot be produced. However, cryptostomes and fenestrates are double-walled stenolaemates with calcified zooid frontal walls that are interior walls and were capable of adding calcification to their outer surfaces. *A. orodamnus* clearly belongs to one of these groups. Among Ordovician genera, only arthrostylid cryptostomes (e.g. *Nematopora* Ulrich, 1888) and the fenestrate genus *Enallopora* d'Orbigny, 1849 closely resemble *A. orodamnus*. However, branches of arthrostylids tend to be straighter and do not develop the same amount of proximal thickening as *A. orodamnus*. Furthermore, *A. orodamnus* shows no indications of the uncalcified articulations found in most arthrostylids. The affinities of *Alwynopora* with the Order Fenestrata are indicated by a combination of three features: restriction of zooecial apertures to one side only of the branches, unjointed branches, and proximally thickened branches.

Enallopora, together with its subjective junior synonym *Protocrisina* Ulrich, 1889, has a branching pattern like that of *A. orodamnus* but the branches bear three or four rows of zooecial apertures, often with small 'accessory pores' between them. Elsewhere in the Order Fenestrata different generic names are accorded to taxa having two and more than two rows of zooecial apertures. These may reflect important differences in budding pattern. Therefore, distinction between *Enallopora* and *Alwynopora* is justified, although a close relationship between the two genera seems likely. Some species of *Enallopora*, such as *E. oeilensis* (Wiman, 1902) from the Ashgill of Sweden, exhibit proximal branch thickening of a similar magnitude to *A. orodamnus* (see Brood 1982, fig. 7A and F). *Enallopora* is unusual among fenestrates in lacking styles within the laminated skeleton (F. K. McKinney,
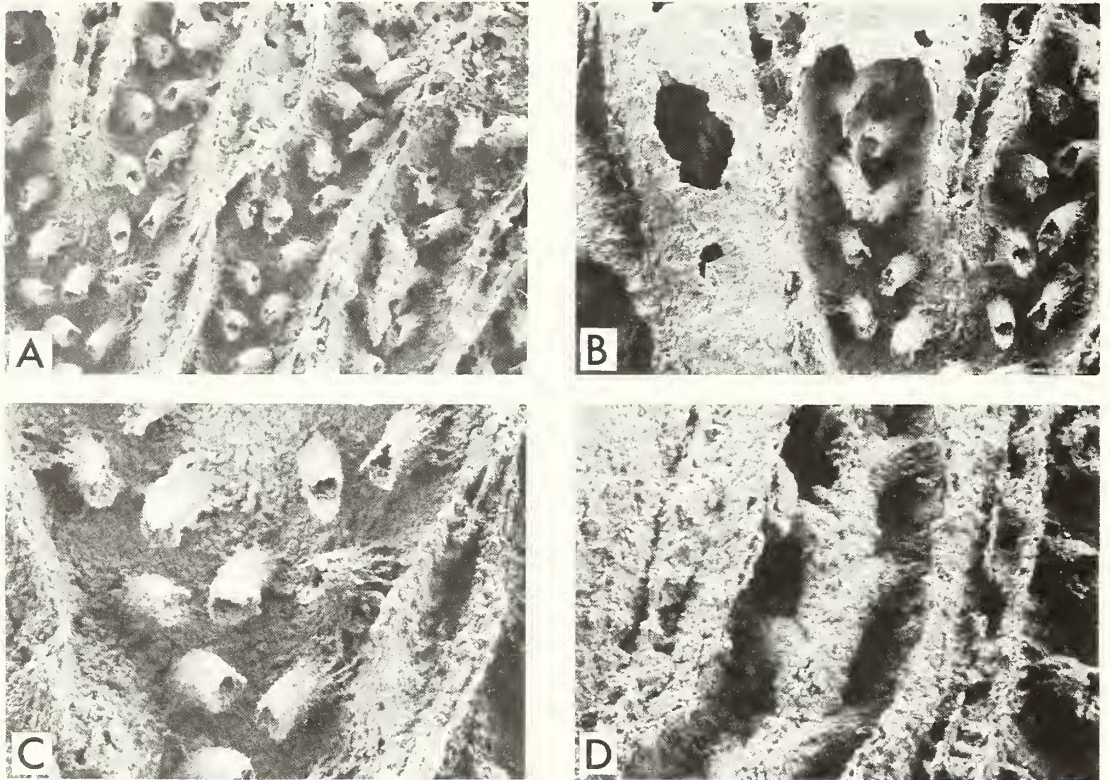
TEXT-FIG. 4. *Alwynopora orodamnus* sp. nov., thick proximal branches with silicification of internal structure, BM(NH) PD6272. Scanning electron micrographs of reverse surface of uncoated specimen using back-scattered electrons. A, closely spaced branches with basal walls removed and silicification of distal parts of zooecial linings, ×14; B, branches with basal walls intact (left) and removed, ×16; C, detail of silicification of distal parts of zooecial linings, ×28; D, complete silicification of zooecial linings showing zooecia arising from a budding locus at the centre of the branch, ×31.

pers. comm.). Unfortunately, unsilicified material of *Alwynopora* is not available for comparison of wall microstructure. Though *Enallopora* is usually assigned to the Family Fenestellidae King, 1850 (see Bassler 1953), the atypical microstructure may justify revival of the Family Enalloporidae Miller, 1889 to which *Alwynopora* is also tentatively assigned.

Discussion. The silicified preservation of *A. orodamnus* necessitates some interpretation as a preliminary to reconstruction of original skeletal morphology. In some specimens only the outer surfaces of the branches have been silicified so that acid treatment leaves specimens as hollow tubes lacking internal structure (text-fig. 5). Tavener-Smith (1973) reported similar preservation of Carboniferous fenestrates where silicification evidently progressed from the outside of the branches inward. In other specimens of *A. orodamnus*, however, silicification is more extensive and includes zooecial linings. The void between these linings and the outer branch surface represents unsilicified skeleton (text-fig. 5). These specimens are valuable in revealing details of internal structure including zooecial shape, dimensions, and budding pattern.

partially silicified
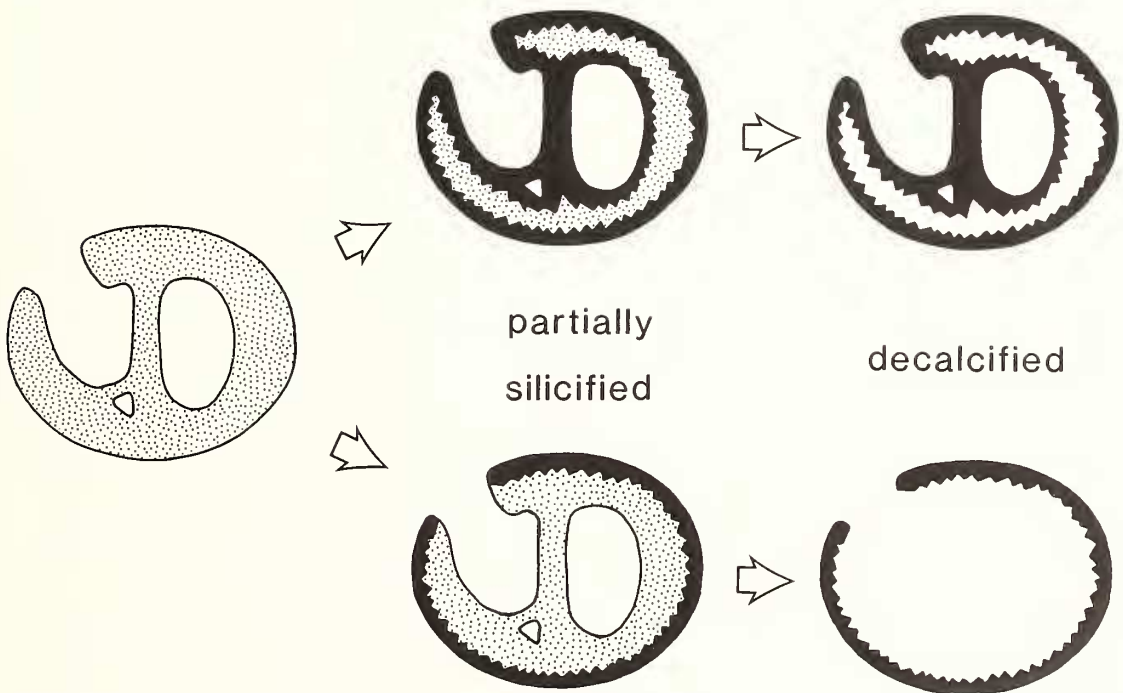
decalcified

TEXT-FIG. 5. Interpretation of silicification in *Alwynopora orodamnus* sp. nov. shown in transverse section. Calcified parts are stippled, silicified parts are black. Silicification occurs as a rind replacing the outer surface layers of skeleton and sometimes (upper sequence) the lining of the zooecial chambers.

The high degree of variability in branch thickness between specimens of *A. orodamnus* also warrants comment. Variation is continuous and there is no indication that more than one species is present at Tourmakeady. Thin and thick branches have the same alternating biserial arrangement of apertures with equivalent interapertural spacing. A gentle but distinct distal taper in some branch lengths (e.g. text-fig. 3c) is evidence that branch thickness is age-related. Young branches are narrow and have thin walls and sinuous margins (e.g. text-fig. 2c). During growth addition of calcification to the outer surfaces of branches resulted in substantial branch thickening and loss of sinuosity (text-fig. 4). This was accompanied by lengthening of zooecial chambers, divergence of apertures

DISTAL BRANCH   PROXIMAL BRANCH

external

tangential

section

transverse

section

1mm
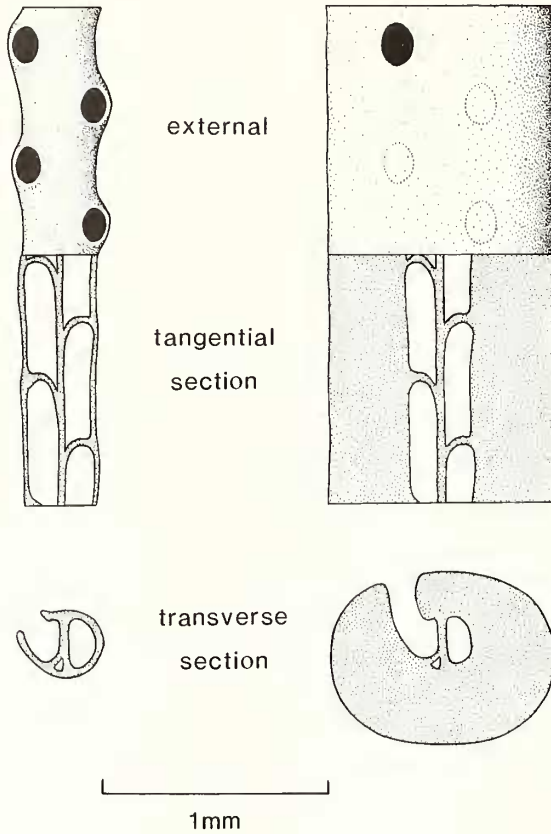
TEXT-FIG. 6. Diagrammatic reconstruction
of morphology in a distal branch (young)
and a proximal branch (old) of *Alwynopora
orodamnus* sp. nov. Calcified wall is evenly
stippled in the tangential and transverse
sections.

from the branch midline, and by the formation of diaphragms over zooecial apertures (assuming
aperture occlusion is not a preservational artefact).

An important consequence of branch thickening was the reduction and eventual elimination of the
spaces between adjacent branches (e.g. text-fig. 4). As fenestrate bryozoans are thought to have
generated feeding currents that drew water towards the frontal surface of branches and expelled
filtered water through the spaces between branches and towards their reverse surface (Cowen and
Rider 1972; Taylor 1979), occlusion of the spaces between branches during colony growth may have
impaired feeding. However, basal regions of bryozoan colonies (e.g. adeoniform cheilostomes, see
Cheetham and Thomsen 1981) may be occupied by zooids which have lost their feeding function. The
same is likely for *A. orodamnus* colonies, especially if zooecial apertures in basal branches were closed
by diaphragms. Basal branches of *A. orodamnus* may have fulfilled a supportive function. For this
role the kind of thick calcification present in many colonies would have been advantageous in
resisting bending stresses imposed by water movement around the colony (cf. adeoniform
cheilostomes, see Cheetham and Thomsen 1981).

LOWER ORDOVICIAN BRYOZOA

Discovery of the first fenestrate bryozoan in the lower Ordovician prompts a brief review of world-
wide records of lower Ordovician Bryozoa. As yet there are no unequivocal bryozoans of pre-Arenig

age (Taylor 1984), but by the late early Ordovician a moderately diverse bryozoan fauna had become established. Table 1 summarizes the bryozoan taxa recorded from the lower Ordovician with their stratigraphical occurrence and provenance. This table is the basis for the following comments on taxonomic distribution, morphological diversity, and palaeogeographical distribution. The lower–middle Ordovician boundary is here placed at the top of the Arenig Series in Britain (Williams *et al.* 1972), very approximately equivalent to the top of the Volkhov Stage (B2) in Estonia, and the top of the Valhallen Stage in North America (Fortey 1980).

Taxonomic distribution

A striking feature of the thirty-eight species recorded from the lower Ordovician is their wide taxonomic distribution (Table 1). All five orders of stenolaemate bryozoans recognized in the revised bryozoan *Treatise* (Boardman *et al.* 1983) are represented. Given the uncertainties in correlation within the lower Ordovician, one may conclude that stratigraphical evidence on the relative time of appearance of the orders is never likely to be of value in resolving phylogenetic relationships at ordinal level. A smaller proportion of taxa have lower Ordovician representatives at successively lower taxonomic levels. Three of twelve (25%) cystoporate families (Utgaard *in* Boardman *et al.* 1983) are known from the lower Ordovician, eight of nineteen (42%) trepostome families (Astrova 1978, with the addition of the Dianulitidae), and two of thirteen (15%) cryptostome families (Karklins *in* Boardman *et al.* 1983; Blake *in* Boardman *et al.* 1983); lack of up-to-date information on fenestrate and cyclostome classification precludes their analysis. At the genus level the lower Ordovician has only four of ninety (4%) cystoporate genera, eleven of eighty-seven (13%) trepostome genera, and three of eighty (4%) cryptostome genera. Such early diversification at high taxonomic levels is also a feature of many phyla other than the Bryozoa. However, unlike some phyla (notably the Echinodermata, see Paul 1979) many of the higher taxa established during early bryozoan evolution were of long duration. All five stenolaemate orders persisted throughout the Palaeozoic at least.

Another aspect of the data (Table 1) is the considerable contribution of trepostomes to the early diversification of the Bryozoa. This early trepostome dominance was eroded somewhat during the middle Ordovician when other orders, especially the Cryptostomata (e.g. Ross 1964), became more important. However, palaeogeographical distribution may be a major factor in this apparent evolutionary pattern. Most lower Ordovician bryozoans come from the trepostome-dominated region of Estonia whereas younger faunas are known also from regions of markedly different faunal composition, e.g. the middle to upper Ordovician of the Siberian Platform where trepostomes are scarce and ptilodictyine cryptostomes dominate (Nekhoroshev 1961).

Morphological diversity

Lawood and Taylor (1979) have already emphasized the wide variety of colony-forms present in bryozoans of the Ordovician as a whole and their possible ecological significance. Many of these colony-forms were established during early Ordovician times. Dome-shaped colonies (e.g. *Revalotrypa gibbosa*) are particularly prevalent but also present in the lower Ordovician are cylindrical branched colonies of several types (e.g. *Wolinella baltica, A. orodannus, Dittopora annulata*), frondose colonies (e.g. *Trepocryptopora dichotomata*), and laminate colonies (e.g. *Ceramopora? unapensis*). Subdivision of colonies into subcolonies (cormidia) is known from lower Ordovician bryozoans, notably *Dianulites hexaporites* and the dianulitid described by McLeod (1978). Other morphological characters (many used taxonomically) include laminar and granular wall structures, acanthostyles, interzooidal communication pores, diaphragms, hemiphragms, interzooidal vesicles, lunaria, calcified exterior walls, and various types of zooidal polymorph. An analysis of the distribution of these and other characters would clearly be of value in resolving phylogenetic relationships. Lower Ordovician representatives of each stenolaemate order may be expected to possess a high proportion of morphological characters in primitive states. This could assist the distinction between primitive and advanced character states which is important in reconstructing phylogeny within each stenolaemate order.

TABLE 1. Records of bryozoans from the lower Ordovician

Taxon	Stratigraphy	Locality	Reference
ORDER CYCLOSTOMATA			
Family Corynotrypidae			
Wolinella baltica Dzik	M. Volkhov Stage	Estonia; Poland	Dzik 1981
ORDER CYSTOPORATA			
Family Ceramoporidae			
Ceramopora? unapensis Ross	Kindblade Fm.	Oklahoma	Ross 1966
Family Anolotichiidae			
Lamtshinopora hirsuta Astrova		Vaigach Is., U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Profistulipora arctica Astrova		Novaya Zemlya, U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Profistulipora retrusa Astrova		Novaya Zemlya, U.S.S.R.	Astrova 1965; Utgaard in Boardman *et al.* 1983
Family Xenotrypidae			
Xenotrypa primaeva (Bassler)	Volkhov Stage	Estonia	Bassler 1911; Utgaard in Boardman *et al.* 1983
ORDER TREPOSTOMATA			
Family Esthonioporidae			
Esthoniopora communis Bassler	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Esthoniopora lessnikovae (Modz.)	Volkhov Stage	Estonia	Modzalevskaya 1953; Mannil 1959
Esthoniopora curvata Bassler	Volkhov Stage	Estonia	Mannil 1959
Family Orbiporidae			
Orbipora solida Bassler	Volkhov Stage	Estonia	Modzalevskaya 1959
Orbipora acanthopora Bassler	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Dittoporidae			
Dittopora clavaeformis Dybowski	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Dittopora annulata (Eichwald)	Volkhov Stage	Estonia	Bassler 1911; Modzalevskaya 1953
Dittopora ramosa Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Dittopora sokolori Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Hemiphragma rotundatum Bassler	Volkhov Stage	Estonia	Modzelevskaya 1953
Family Halloporidae			
Diplotrypa petropolitana Nicholson	Volkhov Stage	Estonia	Bassler 1911
Diplotrypa bicornis (Eichwald)	Volkhov Stage	Estonia	Bassler 1911
Family Trematoporidae			
Revalotrypa gibbosa (Bassler)	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Nicholsonella huoi Yang	U. lower Ord.	Liangshan, China	Yang 1957
Nicholsonella papillaris Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Nicholsonella rotundicellularis Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Nicholsonella arborea Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Amplexoporidae			
Anaphragma vetustum Bassler	Volkhov Stage	Estonia	Modzalevskaya 1953
Monotrypa helenae Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Atactotoechidae			
Orbignyella antiqua Modzalevskaya	Volkhov Stage	Estonia	Modzalevskaya 1953
Family Dianulitidae			
Dianulites fastigiatus Eichwald	Volkhov Stage	Estonia	Bassler 1911
Dianulites petropolitana Dybowski	Volkhov Stage	Estonia	Bassler 1911; Modzalevskaya 1953
Dianulites glauconiticus Mannil	Volkhov Stage	Estonia	Mannil 1959
Dianulites janischewskyi Modz.	Volkhov Stage	Estonia	Modzalevskaya 1953
Dianulites hexaporites (Pander)	Volkhov Stage	Estonia	Modzalevskaya 1953
Dianulites multimesoporicus Modz.	Volkhov Stage	Estonia	Modzelevskaya 1953
'Dianulitid'	Cassinian	Arkansas; Missouri	McLeod 1978
ORDER CRYPTOSTOMATA			
Family Arthrostylidae			
Arthroclema cf. *armatun* Ulrich	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Family Stictoporellidae			
Stictoporellina gracilis (Eichwald)	Volkhov Stage	Estonia	Bassler 1911; Mannil 1959
Family incertae sedis			
Trepocryptopora dichotomata Yang	U. lower Ord.	Liangshan, China	Yang 1957; Karklins in Boardman *et al.* 1983
Trepocryptopora flabelata Yang	U. lower Ord.	Liangshan, China	Yang 1957
ORDER FENESTRATA			
? Family Enalloporidae			
Alwynopora orodamnus sp. nov.	U. Arenig	Tourmakeady, Eire	this paper

Palaeogeographical distribution

Lower Ordovician bryozoans are known from three main palaeogeographical regions: the Baltic Plate (Estonia and Novaya Zemlya), the North American Plate (Tourmakeady and localities in the U.S.A.), and the Yangtze Plate (Liangshan). During Arenig times the Baltic Plate is likely to have been temperate (Cocks and Fortey 1982), the North American Plate tropical (Scotese *et al.* 1979), and the Yangtze Plate tropical or subtropical (R. A. Fortey, pers. comm. 1983). These three plates were widely separated, demonstrating the wide distribution of bryozoans in the early Ordovician. This substantial geographical spread in conjunction with the taxonomic variety of Arenig bryozoans points to a considerable pre-Arenig history that is as yet unknown and may be crucial to the testing of various models (e.g. Larwood and Taylor 1979; Taylor 1981) of early bryozoan diversification.

REFERENCES

ASTROVA, G. G. 1965. Morphology, evolutionary history, and systematics of Ordovician and Silurian bryozoans. *Trudy paleont. Inst.* **106**, 1–432. [In Russian.]
—— 1978. The history of development, system and phylogeny of Bryozoa. Order Trepostomata. Ibid. **169**, 1–240. [In Russian.]
BASSLER, R. S. 1911. The early Paleozoic Bryozoa of the Baltic Provinces. *Bull. U.S. natn. Mus.* **77**, 1–382.
—— 1953. Bryozoa. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*, Part G, 1–253. Geol. Soc. of Amer. and Univ. Kansas Press, New York and Lawrence.
BOARDMAN, R. S., CHEETHAM, A. H., BLAKE, D. B., UTGAARD, J., KARKLINS, O. L., COOK, P. L., SANDBERG, P. A., LUTAUD, G. and WOOD, T. S. 1983. Bryozoa. *In* ROBISON, R. A. (ed.). *Treatise on invertebrate palaeontology*, part G. Revised, vol. 1, 625 pp. Geol. Soc. of Amer. and Univ. Kansas Press, Boulder and Lawrence.
BORG, F. 1926. Studies on Recent cyclostomatous Bryozoa. *Zool. Bidr. Upps.* **10**, 181–507.
BROOD, K. 1982. Ashgill Bryozoa from a fissure filling at Solberga, Dalarna. *Geol. För. Stockh. Förh.* **104**, 167–181.
CHEETHAM, A. H. and THOMSEN, E. 1981. Functional morphology of arborescent animals: strength and design of cheilostome bryozoan skeletons. *Paleobiology*, **7**, 355–383.
COCKS, L. R. M. and FORTEY, R. A. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. *J. geol. Soc. Lond.* **139**, 465–478.
COWEN, R. and RIDER, J. 1972. Functional analysis of fenestellid bryozoan colonies. *Lethaia*, **5**, 145–164.
CURRY, G. B. 1981. Variable pedicle morphology in a population of the Recent brachiopod *Terebratulina septentrionalis*. Ibid. **14**, 9–20.
—— 1983. Ecology of the Recent deep-water rhynchonellid brachiopod *Cryptopora* from the Rockall Trough. *Palaeogeogr., Palaeoclimat., Palaeoecol.* **44**, 93–102.
—— INGHAM, J. K., BLUCK, B. J. and WILLIAMS, A. 1982. The significance of a reliable Ordovician age for some Highland Border rocks in Central Scotland. *J. geol. Soc. Lond.* **139**, 451–454.
DEWEY, J. F., RICKARDS, R. B. and SKEVINGTON, D. 1970. New light on the age of Dalradian deformation and metamorphism in Western Ireland. *Norsk. geol. Tidsskr.* **50**, 19–44.
DZIK, J. 1981. Evolutionary relationships of the early Palaeozoic 'cyclostomatous' Bryozoa. *Palaeontology*, **24**, 827–861.
ELIAS, M. K. and CONDRA, G. E. 1957. *Fenestella* from the Permian of West Texas. *Geol. Soc. Am. Mem.* **70**, 1–158.
FORTEY, R. A. 1980. The Ordovician of Spitsbergen, and its relevance to the base of the Middle Ordovician in North America. *In* WONES, D. R. (ed.). *The Caledonides in the USA. Memoir*, **2**, Department of Geological Sciences, Virginia Polytechnic Institute and State University.
GARDINER, C. I. and REYNOLDS, S. H. 1909. On the igneous and associated sedimentary rocks of the Tourmakeady district (Co. Mayo), with a palaeontological appendix by F. R. C. Reed. *Q. Jl geol. Soc. Lond.* **65**, 104–156.
———— 1910. The igneous and associated sedimentary rocks of the Glensaul district (Co. Galway) with a palaeontological appendix by F. R. C. Reed. Ibid. **66**, 253–279.
LARWOOD, G. P. and TAYLOR, P. D. 1979. Early structural and ecological diversification in the Bryozoa. *In* HOUSE, M. R. (ed.). *The origin of major invertebrate groups*, 209–234. Academic Press, London.

MCLEOD, J. D. 1978. The oldest bryozoans: new evidence from the early Ordovician. *Science, N. Y.* **200**, 771–773.

MANNIL, R. M. 1959. Problems in the stratigraphy and Bryozoa of the Ordovician of Estonia. *Dokl. Akad. Nauk. Estonia SSSR*, 1959, 1–39. [In Russian.]

MILLER, S. A. 1889. *North American geology and paleontology*, 664 pp. Cincinnati.

MODZALEVSKAYA, E. A. 1953. Order Trepostomata of the East Baltic area and their stratigraphical importance. *Trudy Vses. neft. nauchno-issled. geol.-razv. Inst.* **78**, 91–167. [In Russian.]

NEKHOROSHEV, V. P. 1961. Ordovician and Silurian Bryozoa of the Siberian Platform, Order Cryptostomata. *Trudy Vses. nauchno-issled. geol. Inst.*, N.S. **41** (2), 1–246. [In Russian.]

ORBIGNY, A. C. D'. 1849. Description de quelques genres nouveaux de Mollusques bryozoaires. *Revue Mag. Zool.* (2), **1**, 499–504.

PAUL, C. R. C. 1979. Early echinoderm radiation. *In* HOUSE, M. R. (ed.). *The origin of major invertebrate groups*, 415–434. Academic Press, London.

ROSS, J. P. 1964. Morphology and phylogeny of early Ectoprocta (Bryozoa). *Geol. Soc. Am. Bull.* **75**, 927–948.

—— 1966. Early Ordovician ectoproct from Oklahoma. *Okla. Geol. Notes*, **26**, 218–224.

SCOTESE, C. R., BAMBACH, R. K., BARTON, C., VAN DER VOO, R. and ZIEGLER, A. M. 1979. Paleozoic base maps. *J. Geol.* **87**, 217–277.

TAVENER-SMITH, R. 1973. Fenestrate Bryozoa from the Visean of County Fermanagh, Ireland. *Bull. Br. Mus. nat. Hist.* (Geol.), **23**, 389–493.

TAYLOR, P. D. 1979. The inference of extrazooidal feeding currents in fossil bryozoan colonies. *Lethaia*, **12**, 47–56.

—— 1981. Functional morphology and evolutionary significance of differing modes of tentacle eversion in marine bryozoans. *In* LARWOOD, G. P. and NIELSEN, C. (eds.). *Recent and Fossil Bryozoa*, 235–247. Olsen and Olsen, Fredensborg.

—— 1984. *Marcusodictyon* Bassler 1952 from the lower Ordovician of Estonia: not the earliest bryozoan but a phosphatic problematicum. *Alcheringa*. **8**.

WILLIAMS, A. and CURRY, G. B. 1984. Lower Ordovician Brachiopoda from the Tourmakeady Limestone, Co. Mayo, Eire. *Bull. Br. Mus. nat. Hist.* (Geol.) **35**.

—— STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D. and WHITTINGTON, H. B. 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.* **3**, 1–74.

WIMAN, C. 1902. Über die Borkholmer Schicht in Mittelbaltischen Silurgebiet. *Bull. geol. Instn. Univ. Uppsala*, **5**, 149–217.

YANG, K.-C. 1957. Some Bryozoa from the upper part of the Lower Ordovician of Liangshan, Southern Shensi (including a new genus). *Acta palaeontol. Sinica*, **5**, 1–10. [In Chinese with an English summary.]

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